

ABUNDANCE AND DISTRIBUTION OF BEAVER

AND COYOTE WILLOW IN GRAND

CANYON, ARIZONA

BY

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SUBMITTED TO

Resource Management
Grand Canyon National Park
Grand Canyon, Arizona
86023

May 18, 1983

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*This is really good
I think you need to make a
stronger case on the relationship between
resistivity and the alluvial deposits
by bringing in the appropriate
hydrological model*

INTRODUCTION

The riparian zone along the Colorado River in Grand Canyon National Park is of great interest to biologists, geologists, and resource managers.]

Since the completion of Glen Canyon Dam in 1963 a number of substantial changes in the fluvial characteristics and riparian vegetation have occurred ^{along the Colorado in GC} (Howard and Dolan 1981, Carothers et al. 1976, Turner and Karpiscak 1980). The work of these authors strongly supports the hypothesis that structure and composition of riparian communities is closely linked to the fluvial and geomorphological characteristics of the Colorado River. The precise nature of this relationship has not been elucidated. Likewise, the stability of species ^{plants/animals??} dwelling in riparian habitats remains poorly understood.

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The objectives of this study are to analyze the changes in abundance and distribution of beaver (Castor canadensis) and coyote willow (Salix exigua Nutt.) which have occurred between 1979 and 1983 along the upper Colorado River in Grand Canyon. This reach of river cuts through 12 major geological formations between Lees Ferry (R.M. 0) and Phantom Ranch (R.M. 87.6). Hence, ^{which data?} these data also permit analysis of the response of two obligate riparian species to geomorphology of the floodplain and other environmental conditions. Sufficient data of this sort would permit modelling future population trends of beaver and coyote willow in relation to environmental perturbations. The present data base is inadequate.

METHODS AND MATERIALS

During April and May of 1979 I censused beaver between Lees Ferry and Diamond Creek (R.M. 225.6). Beaver were censused by counting burrow entrances and food caches from a boat during a period of low releases. Binoculars were used to make observations. In February 1983 I repeated this census between Lees Ferry and Phantom Ranch. Raw data were grouped into 'burrow complexes' occupied by a minimum of one pair of beaver. The results represent the number of burrow complexes present in the study area. These groupings reflect the consensus of the literature on behavior and life history of beavers (Jenkins and Busher 1979 and references therein). Within a burrow complex and the surrounding territory (sensu stricto), a monogamous adult pair, yearlings and kits comprise an extended family. Young disperse at approximately 2 years of age and breed at three. Breeding occurs in January and February (Jenkins and Busher 1979, Svendsen 1980). In the western U.S., average litter size varies from 2.06 to 4.40. Variation in average litter size reflects habitat quality. Generally, large litters characterize cottonwood and aspen dominated habitats; smaller litters are produced in willow habitats (Huey 1956, Rutherford 1964).

During the summer of 1979 I mapped the abundance and distribution of coyote willow between Lees Ferry and Diamond Creek. Observations were made from a boat using binoculars and verified by ground truthing. The location and extent of each

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willow stand was recorded on a vegetation map of the study area. In the lab I drew lines perpendicular to the river at 1/10 mile intervals. This permitted calculation of two measures of willow abundance and distribution. First, the number of 1/10 mile sections containing willows (NUMBER OF ENCLOSURES) may be enumerated. I also counted the number of discrete coyote willow stands (NUMBER OF PATCHES). These data are summarized for 1979 and 1983 in each of 12 major rock groups between Lees Ferry and Phantom Ranch. *

Based on geological observations (LaRue 1925, Hamblin and Rigby 1968, Howard and Dolan 1981) each rock formation was classified as to its resistance to erosion (RESISTIVITY). This provides a basis for natural divisions based on parent materials (Table 1). All but two of the 12 strata are recognized geological formations. The Supai ^{formation} ~~sandstone~~ and Grand Canyon series are more finely subdivided by most geologists. Beaver and coyote willow responded uniformly to all the strata of massive, homogeneous sandstone ^{mudstone, siltstone, limestone} which I refer to as the Supai. Although some members of the Grand Canyon series are more resistant to erosion than others, the reaches of river in which resistant members are exposed are an insignificant portion of the entire group which is easily eroded. No distinguishable variation occurs in functional response of willow abundance and distribution in the reach dominated by the Grand Canyon series. Finally, the nature of the Muav limestone in the upper canyon is different from that downstream from Phantom Ranch (Howard and Dolan 1981). In this paper I classified the Muav

* while reading me I had trouble with the meaning of Enclosures this is my 2nd reading, and there may be a better word??

TABLE 1. Major geologic formations encountered on the Colorado River between Lees Ferry and Phantom Ranch, Grand Canyon, Arizona (from Hamblin and Rigby 1968).

<u>RIVER MILE</u>	<u>FORMATION</u>	<u>RESISTIVITY</u>
0 - 1.0	Shinarump	High
1.0 - 1.7	Kaibab	High
1.7 - 3.9	Toroweap	High
3.9 - 5.2	Coconino	High
5.2 - 11.2	Hermit	Low
11.2 - 22.6	Supai*	High
22.6 - 35.9	Redwall	High
35.9 - 51.8	Muav*	Intermediate
51.8 - 59.0	Bright Angel	Low
59.0 - 63.5	Tapeats	Intermediate
63.5 - 77.4	Grand Canyon Series*	Low
77.4 - 87.6	Granite/Schist	High

*see text for comments relative to these formations

as being of intermediate resistivity. Between R.M. 35.9 and R.M. 51.8 the Muav forms numerous small shelves and is much less massive than that encountered downstream.

Data were analyzed by a series of χ^2 tests for independent samples (Seigel 1956). I tested the hypothesis that reaches of the Colorado River banded by rocks of three resistivity classes did not differ with respect to distribution of beaver and willow.

in introduction

RESULTS AND DISCUSSION

FLOODPLAIN CHARACTERISTICS

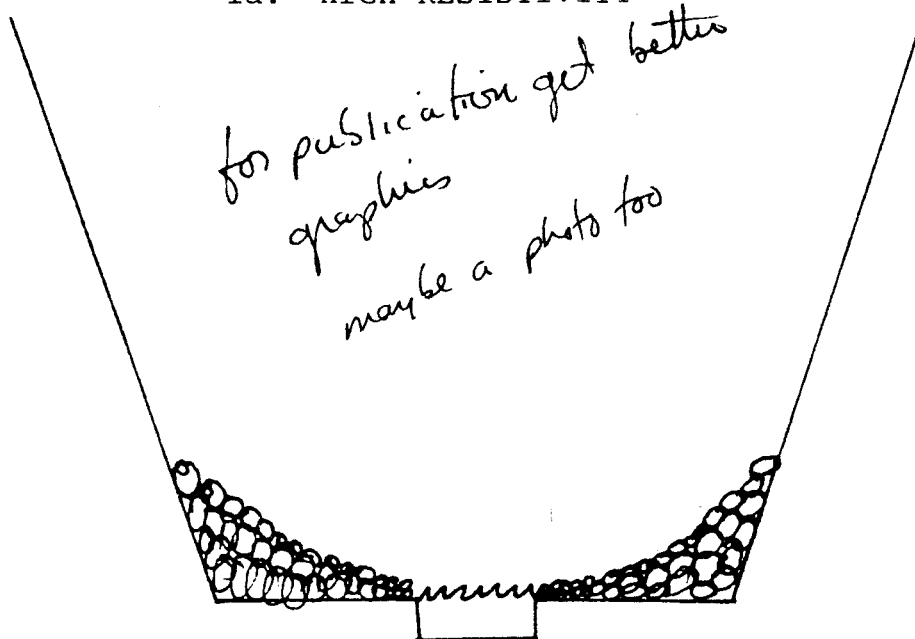
The term 'floodplain' is, strictly speaking, not applicable to fluvial deposits along the upper Colorado River as the floodplain is presently not subject to periodic inundation. Flows are presently regulated at Glen Canyon Dam. Nonetheless, I use the term here to describe Zones 2 - 4 of Carothers et al. (1976) which are colonized by riparian plants. Prevalent taxa include four species of baccharis (Baccharis sarothroides Gray, B. sergiloides Gray, B. salicifolia (R. & P.) Pers., and B. emoryi Gray), arrowweed (Tesseria sericea (Nutt.) Shinnars), tamarix (Tamarix chinensis Lour.), coyote willow, and mesquite (Prosopis glandulosa var. torreyana (Benson) M.C. Johnst.).

Prior to the completion of Glen Canyon Dam in 1963, the major influence on distribution and development of riparian vegetation was the pattern and volume of mainstream flows. Since 1963, monthly and seasonal discharge patterns have been

relatively stable (Figures 3 and 4 in Turner and Karpiscak 1980). However, diurnal variations in discharge have become more pronounced (Figure 2 in Turner and Karpiscak 1980). Today, the major factor influencing riparian vegetation is stream gradient. Leopold (1969) found that most of the change in elevation between Lees Ferry (ca. 3100') and Lake Mead (ca. 900') occurs in about 10 percent of the total distance (280 miles). Generally, the largest drops occur in rapids. Channel gradient has considerable influence on several factors which regulate discharge-width, depth, and velocity of water in a channel (Hupp, 1982). Ultimately, stream gradient is controlled by the lithology of the strata through which a channel flows. Structural control of this sort is extremely apparent in Grand Canyon.

Resistivity of major rock groups between Lees Ferry and Phantom Ranch (Table 1) do not conform exactly to those proposed by Howard and Dolan (1981). This is due to an apparent lack of functional response by beavers and coyote willows to variations in lithology. Four channel types are present in Grand Canyon (Howard and Dolan 1981). Three are found in the study reach. In reaches of the river with high gradient, flood-plain deposits are usually lacking and the channel is narrow (e.g. R.M. 76.5-87.6). Highly resistant rock strata border the river and form steep cliffs (Figure 1a). Reaches characterized by an intermediate gradient have a relatively wide channel and deposition of fluvial sediments occurs on tributary fans and in eddies below the fans (e.g. R.M. 59.0-63.5).

1a. HIGH RESISTIVITY



1b. LOW RESISTIVITY

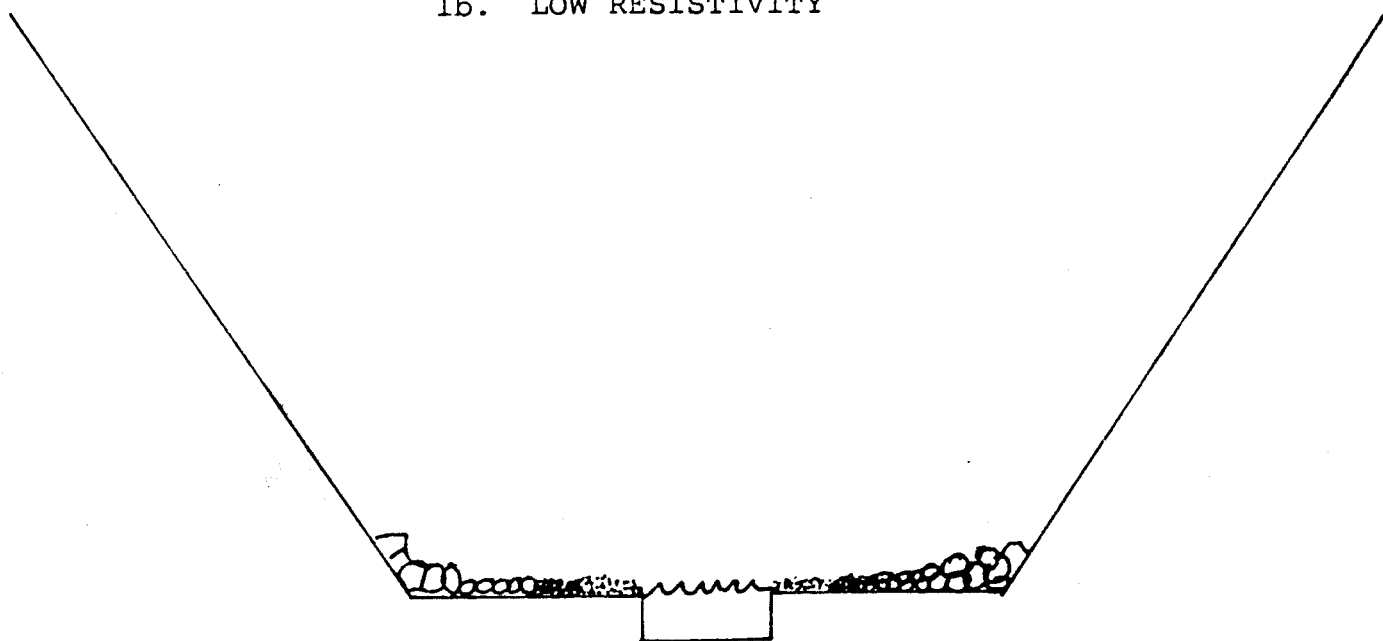


FIGURE 1. Diagrammatic cross-section of channels through high resistivity (a) and low resistivity (b) strata on the Colorado River between Lees Ferry and Phantom Ranch, Grand Canyon National Park, Arizona.

Rocks at river level are usually resistant sandstones or limestones which may form steep cliffs. Low gradient reaches are characterized by a widechannel, broad floodplain, and large deposits of sediments (e.g. R.M. 51.8-59.0). These reaches are in rock strata which are easily eroded and form a characteristic channel configuration (Figure 1b).

BEAVER ABUNDANCE AND DISTRIBUTION

The 1979 census includes the 225.6 miles of river between Lees Ferry and Diamond Creek. One hundred burrow complexes were located, of which 70 were between Lees Ferry and Phantom Ranch. Beavers are not evenly distributed throughout Grand Canyon. I tested the association between beaver distribution and available habitat in each category of resistivity between Lees Ferry and Phantom Ranch. The purpose of the analysis is to assess the role of resistivity of bedrock in regulation of beaver distribution. First, I tested the null hypothesis that there is no relationship between beaver distribution and available habitat characterized by bedrock of low and intermediate resistivity. The null hypothesis cannot be rejected (Table 2, $\chi^2 = 0.30$ with 1 df, $p > 0.50$). This result suggests that beavers do not discriminate between habitats with bedrock of low and intermediate resistivity. The data from these two habitats were lumped and compared with beaver distribution on strata with high resistivity. I tested the null hypothesis that there is no relationship between beaver distribution and available habitat characterized by bedrock of low and high resistivity.

TABLE 2. Distribution of beaver (Castor canadensis) burrow complexes in relation to the resistivity of bedrock at river level, Grand Canyon National Park, Arizona. Data were gathered between Lees Ferry and Phantom Ranch during April 1979.

	RESISTIVITY		
	--	0	+
NUMBER OF BURROW COMPLEXES	31	29	10
NUMBER OF MILES OF AVAILABLE HABITAT	27.1	20.4	40.1

The null hypothesis is rejected (Table 2, $\chi^2 = 17.92$ with 1 df, $p < .001$). There is a significant association between habitats characterized by bedrock of low resistivity and beaver distribution. Thirty one percent of the 87.6 miles from Lees Ferry to Phantom Ranch are through the least resistant bedrock. This 31 percent of the total habitat supports 44 percent of the burrow complexes.

The sites suitable for burrows are limited in Grand Canyon. Several features characterize all burrow sites; including still water at the mouth of the burrow and sufficient depths of consolidated, fine-grained sediments. These sites are concentrated in reaches of the Colorado flowing through rock formations of low and intermediate resistivity, having a low stream gradient and a wide floodplain. Howard and Dolan (1981) report a complex pattern of variation between bedrock resistivity, valley width, and other fluvial attributes of the Colorado River.

Beavers are ^{apparently} ~~either very accomplished geomorphologists or~~ extremely sensitive to a suite of habitat variables like resistance of bedrock, channel width, stream gradient, and composition of sediment deposits.

Beavers are monogamous, territorial, and relatively long-lived. They exhibit delayed reproduction (Svendsen 1980). These life history characteristics, acting in concert with the physical constraints just discussed, impose an upper limit on the abundance and distribution of beavers in Grand Canyon. During the last several years beavers appear to have become more abundant in certain tributaries (notably Bright Angel

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Paul Aiken may have numbers

Creek). Given this observation, it is logical to predict that beaver abundance in the mainstream has also increased from 1979 to 1983. High discharge hindered censuses in some reaches during 1983. However, the results (Table 3) show that beaver abundance has been remarkably static since 1979. Two reaches show slight declines and two show increases in the number of burrow complexes. The fifth remained essentially unchanged. An estimated 47 burrow complexes were present in 1979 while 46 were present in 1983 (Table 3).

These results reflect physical constraints of the habitat and peculiarities of beaver biology which place an upper limit on abundance of these mammals in Grand Canyon riparian habitats. Further, the static nature of beaver abundance from 1979 to 1983 indicates that suitable habitat is saturated.

The implication of these observations is that live capture of nuisance beavers on tributaries and subsequent release along the mainstream Colorado are of limited value. Transplanted individuals may disrupt social organization at existing burrow complexes or die because suitable burrow sites and/or food are lacking. It is highly probable that the majority of 'problem' animals in tributaries are young animals (ca. 2 years) recently disperses from parental territories. These animals should weigh between 20 and 27 pounds. If this is the case, the argument that suitable habitats for beaver are at carrying capacity is supported. If these beavers are to be managed, a more practical approach may be a reduction program aimed at destroying animals in situ or live-trapping and relocation outside the park.

Where did this little management tidbit come from?
use it later.

TABLE 3. Number of beaver (Castor canadensis) burrow complexes in selected reaches of the Colorado River, Grand Canyon National Park, 1979 and 1983.

REACH	1979	1983
R.M. 20.0 - R.M. 37.6	5	3
R.M. 37.6 - R.M. 47.3	16	11
R.M. 47.3 - R.M. 58.3	15	14
R.M. 58.3 - R.M. 65.6	6	9
R.M. 71.9 - R.M. 76.5	5	9
TOTAL	47	46

Finally, I note that beavers and their food sources (cottonwoods, willows, aspens, etc.) have a long evolutionary history. Several studies have shown that local extinctions of food plants may result in local extinctions of beavers (Gese and Shadle 1943, Neff 1959). Cyclical local extinctions may be important processes in the life history of beavers and cottonwoods. Cottonwoods along Bright Angel Creek may, in the long run, benefit from periodic irruptions of beaver.

COYOTE WILLOW ABUNDANCE AND DISTRIBUTION

Willows are not evenly distributed throughout Grand Canyon. I tested the association between willow distribution and available habitat of a particular resistivity between Lees Ferry and Phantom Ranch. The objective of the analysis is to assess the role of resistivity of bedrock in regulation of coyote willow distribution. First, I tested the null hypothesis that there is no relationship between coyote willow distribution and habitats characterized by bedrock of low and intermediate resistivity. The null hypothesis cannot be rejected (Table 4, $\chi^2 = 0.02$ with 1 df, $p > 0.50$). Coyote willows do not show a detectable functional response to colonization of habitats characterized by bedrock of low and intermediate resistivity. The data from these two habitats were lumped and compared to willow distribution in habitats characterized by highly resistant strata. I tested the null hypothesis that there is no relationship between willow distribution and available habitats characterized by bedrock of low and high resistivity. The

TABLE 4. Distribution and abundance of coyote willow (Salix exigua Nutt.) in relation to the resistivity of bedrock at river level, Grand Canyon National Park, Arizona. Data were gathered between Lees Ferry and Phantom Ranch during April 1979.

	RESISTIVITY		
	--	0	+
ENCLOSURES	182	132	57
NUMBER OF MILES OF AVAILABLE HABITAT	27.1	20.4	40.1

null hypothesis is rejected (Table 4, $\chi^2 = 39.51$ with 1 df, $p < .001$). There is a significant association between the habitats characterized by bedrock of low resistivity and coyote willow distribution. Eighty four percent of the enclosures occupied by willows are within the least resistant bedrock which represents only 54 percent of the total available habitat.

Sites suitable for willow colonization are limited in Grand Canyon. Those with least resistant bedrock, low channel gradient, a broad channel, and adequate sediments are optimal habitat of coyote willows on the upper Colorado River. Like their major predator the beaver, willows show a strong positive response to this suite of habitat characteristics.

Coyote willow abundance and distribution have changed most dramatically in those reaches characterized by strata of high resistivity, a steep channel gradient, a narrow channel, and limited fine-grained sediments. This is particularly apparent between R.M. 1 - R.M. 35.9. This reach is marginal habitat for coyote willows. These habitats are likely to be more adversely affected by perturbations than any other. That is, the probability of eliminating coyote willows by perturbing the habitat is greatest here. Successional trends in Grand Canyon riparian communities are uncertain. The existing data base is not of appropriate resolution to permit accurate long range predictions. In general, characteristics of Grand Canyon riparian habitats in 20, 50, or 100 years will be dictated by management objectives of the Bureau of Reclamation with respect to future operating plans for Glen Canyon Dam.

(water release pattern)

this is the first time you mention them not necessary

Distribution and abundance of coyote willows has decreased slightly from 1979 to 1983 (Table 5). There are 876 one-tenth mile sections between Lees Ferry and Phantom Ranch. Forty two percent (371) were occupied by willows in 1979. By 1983, only 37 percent (328) were occupied. Total number of patches declined 35 percent (from 298 to 193) during the same period but it is difficult to determine how many adjacent patches grew together and how many were extirpated. Both processes have occurred but it is likely that the former is more prevalent than the latter, especially within reaches of low and intermediate resistivity.

The number of enclosures in strata of low resistivity decreased 12 percent from 1979 to 1983 (Table 4). Likewise the number of patches in low resistivity strata decreased 27 percent (Table 4). The majority of the decline in both indices is due to a substantial reduction of coyote willows in the Hermit shale (Table 5). This is the only low resistivity reach in which willows have declined. Through the reach where Bright Angel shale occurs at river level, the number of enclosures increased slightly (10 percent) but the number of patches decreased by 13 percent (Table 5). In the reach of river where the Grand Canyon series is at river level, willow abundance and distribution has remained essentially unchanged since 1979 (Table 5). The number of enclosures decreased by only 3 percent and the number of patches decreased by 20 percent.

Reaches dominated by strata of intermediate resistivity showed a 5 percent increase in number of enclosures and a 37

TABLE 5. Distribution and abundance of coyote willow (Salix exigua Nutt.) in Grand Canyon National Park, Arizona, 1979 and 1983

REACH	ROCK FM.	RESISTIVITY	1979		1983	
			ENCLOSURES	PATCHES	ENCLOSURES	PATCHES
R.M. 0.0 - 1.0	Shinarump	+	2	1	6	5
R.M. 1.0 - 1.7	Kaibab L.S.	+	6	4	2	3
R.M. 1.7 - 3.9	Toroweap L.S.	+	17	13	13	11
R.M. 3.9 - 5.2	Coconino S.S.	+	11	15	3	2
R.M. 5.2 - 11.2	Hermit Sh.	-	40	34	17	15
R.M. 11.2 - 22.6	Supai S.S.	+	2	3	0	0
R.M. 22.6 - 35.9	Redwall L.S.	+	19	16	6	4
R.M. 35.9 - 51.8	Muav L.S.	0	103	88	117	52
R.M. 51.8 - 59.0	Bright Angel Sh.	-	40	31	44	27
R.M. 59.0 - 63.5	Tapeats S.S.	0	29	23	21	18
R.M. 63.5 - 77.4	Grand Canyon Ser.	-	102	70	99	56
R.M. 77.4 - 87.6	Schist	+	0	0	0	0

percent decline in the number of patches (Table 5). The number of enclosures in the reach where Muav limestone occurs at river level increased by 14 percent and the number of patches declined by 41 percent. In the Tapeats sandstone, also of intermediate resistivity, the number of enclosures and patches decreased by 25 percent and 22 percent, respectively.

In the most resistant strata, the number of enclosures declined by 47 percent and patches decreased by 52 percent between 1979 and 1983 (Table 5). This habitat had the largest decrease in abundance and distribution of coyote willows recorded during the study. Samples from the Shinarump conglomerate and Kaibab limestone should be treated carefully. Each formation occurs for a fairly short distance along the river and the total number of enclosures and patches in these samples was small in both years. Bearing this in mind, willow abundance and distribution increased in the Shinarump conglomerate and decreased in the Kaibab limestone. In the Toroweap limestone, the number of enclosures declined by 24 percent and patches decreased by 15 percent. Although the Supai ^{formation} sandstone is at river level for approximately 11.4 miles, willows were rare in 1979 (2 enclosures, 3 patches) and absent in 1983. In reaches where Coconino sandstone occurs at river level, enclosures decreased by 72 percent and patches declined by 87 percent between 1979 and 1983. No coyote willows were present in that reach of the river where schist occurs at river level during 1979 or 1983.

→ *Sub heading*
Three major patterns of change in willow abundance and

distribution were apparent - those reaches in which a decrease in number of enclosures and patches occurred (Kaibab, Toroweap, Coconino, Hermit, Supai, Redwall, Tapeats), those reaches in which an increase in number of enclosures and a decrease in number of patches occurred (Muav, Bright Angel), and those characterized by increases in enclosures and patches (Shinarump). A decrease in the number of enclosures and patches suggests a declining coyote willow population. Reaches meeting these criteria are, with two exceptions, in the most resistant strata. These reaches are marginal habitats due to their steep gradient, narrow channel, and poorly developed sediment deposits. Any environmental perturbations exacerbating the impact of these fluvial characteristics will adversely influence willow abundance and distribution in reaches dominated by highly resistant strata. Reasons for the decreases of coyote willows in reaches dominated by Hermit shale and Tapeats sandstone are unclear at this time. In the reach of river where the Grand Canyon series occurs at river level, the decrease in number of enclosures is inconsequential. Patterns of willow distribution in this reach are actually more similar to that in the Muav and Bright Angel where the number of enclosures has increased since 1979 but the number of patches has decreased. Here willow stands are consolidating, characterized by fewer, larger patches in 1983. Patches which were separated four years ago have, in some instances, grown together. The third pattern observed is found only in the area near Lees Ferry where the Shinarump conglomerate occurs at river level. The number of enclosures and

patches has increased. Habitats heretofore unoccupied by coyote willows are being colonized. This pattern is probably related to the width and gradient of the channel through the highly resistant Shinarump. The three patterns are not entirely predictable from a knowledge of the resistivity of a given stratum. This suggests that factors other than resistivity may also influence local abundance and distribution of coyote willows.

*check Dolan et al Science article
re: fault controls... see if you willows
SUMMARY are related to tributaries and
alluvial fans... i.e., take out all data (relative
to resistivity) for willows
new facts etc than
try null hypothesis*

Three channel types are present between Lees Ferry and Phantom Ranch. Channel configuration is regulated by the resistivity of rock formations occurring at river level. The most resistant strata comprise 46 percent of the total habitat. These formations are massive, the river channel is narrow, and it is characterized by a high gradient. Strata of intermediate resistivity make up 23 percent of the total habitat between Lees Ferry and Phantom Ranch. The river channel is relatively wide and may have considerable gradient. Low resistivity habitats represent 31 percent of the total habitat. The river channel is very broad and gradient is low.

Beaver do not discriminate between habitats of low and intermediate resistivity. They prefer these habitats to those with highly resistant rocks at river level. Eighty six percent of all burrow complexes between Lees Ferry and Phantom Ranch are in habitats characterized by low and intermediate

resistivity. This preference is probably related to the availability of suitable burrow sites and food. However, burrow sites may be limited, even in preferred habitats.

Abundance of beavers has not changed substantially from 1979 to 1983. This suggests that physical constraints of the habitat place an upper limit on the abundance of beavers in Grand Canyon. One result of this phenomenon has been an increase of so called beaver depredations along tributary streams. Live-capture and removal of beavers to other areas along the river is not desirable.

Coyote willows do not discriminate between habitats of low and intermediate resistivity. ^{where they} Reaches characterized by strata of low and intermediate resistivity are the preferred habitats of coyote willows. This is probably due to the local development of extensive fine-grained sediment deposits in these reaches.

Willow abundance and distribution ~~declined only slightly~~ from 1979 to 1983. Willows in highly resistivity habitats declined. In habitats of low and intermediate resistivity, willows remained relatively static or expanded slightly.

Present patterns of abundance and distribution of both these obligate riparian organisms are largely due to physical constraints of their habitat. Changes in channel gradient, width, depth, water velocity, and discharge will undoubtedly influence beavers and coyote willows in Grand Canyon National Park.

what about the hydrology? You should have Graff read this

Combine sent.

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~~65-34~~
Havillan

Cladophora Drift and Planktonic Crustaceans
in the Colorado River:
Lee's Ferry to Diamond Creek

Loren R. Haury
Scripps Institution of Oceanography
La Jolla, California

January, 1981

INTRODUCTION

From 18 June until 1 July 1980, the River Unit of the National Park Service, Grand Canyon National Park, conducted a routine patrol of the Colorado River between Lee's Ferry and Diamond Creek, Arizona. Several scientific programs were carried out during the patrol; this report describes the results of two of these. One was an attempt to quantify the drift of the normally attached macroalga, Cladophora glomerata, as a function of distance down river from Lee's Ferry. The second program was a survey of the composition and abundance of planktonic crustaceans found in the Colorado River and some of its tributary terminal pools.

Because of the preliminary nature of these studies, and because of limitations of equipment and time, the same sampling gear was used simultaneously to collect Cladophora and plankton. The experience gained from this trip demonstrated that the techniques were not optimal for either study. The trip also pointed out several scientific problems of relevance, but which could not be approached at the time. Sampling improvements and suggestions for further work are described in the Appendix.

During the sampling period, the flow of the Colorado River, controlled by the discharge from Glen Canyon Dam (Figure 1), was exceptionally variable and, at times, high relative to the conditions existing over the previous years since the closing of the dam. The results presented below may therefore not represent the normal situation for Cladophora transport and

zooplankton presence and abundance.

METHODS

The primary collecting tool for the studies was a 30 cm diameter plankton net with a mesh size of 366 μm . This mesh size collected most of the Cladophora drift and adult and larger juvenile stages of copepods and cladocerans; male cyclopoid copepods were undersampled due to escapement through the mesh. It was large enough to allow passage of most of the suspended sediment load. Occasionally, a net of the same size but with 212 μm mesh was used in places where the sediment load was low. Besides adults, this net collected most naupliar and copepodid stages of the copepods, as well as juvenile instars of cladocerans.

A General Oceanics flow meter in the net mouth measured the volume filtered by each tow. During early tows, river sediment sometimes jammed the meter, resulting in an underestimate of volume filtered. On one occasion, the tow speed was below the threshold speed of the meter; this again resulted in an underestimate of volume filtered.

Tows were taken 1) from boats in the mainstream or its backeddies, 2) from the river bank in the passing mainstream or backeddies, and 3) by pulling the net by hand through tributary pools, either from the bank, from boat, or by walking through the pools pulling the net. Tows from boats and from the edge of the river used a 14 lb depressor to permit fishing the net to near the bottom of the river.

Two tows were taken at each sampling location in the main-

stream and sometimes in tributary pools. Each collection was settled in the plastic jar serving as the cod end. The Cladophora was then removed and weighed in a fine-mesh bag hung from a hand-held Ohaus spring scale (0-50g, 2g divisions) to an accuracy of about $\pm 1g$.

The water and debris remaining in the cod end was then poured through a small 212 μm mesh concentrating net to collect the plankton and free-swimming invertebrate larvae. The invertebrates from both tows were combined and preserved in a single vial with 5% formalin. This technique did not collect all the zooplankton captured by the net, as the sediments and debris were not washed repeatedly before disposal, and the initial removal of Cladophora could have removed some organisms. Thus the results can only be considered as semi-quantitative.

The samples of invertebrates were returned to the laboratory where the separation, identification, and enumeration of crustaceans was made under a binocular microscope. Identification to species and sex was made for all adult crustaceans (except Gammarus lacustris, ostracods, and a chydorid cladoceran). Identifications were made using Pennak (1978) and Ward and Whipple (1959). The number of egg-bearing females was noted, as well as the number of individuals in poor condition. Poor condition was defined as those individuals parasitized by fungus or protists (?), or whose carapaces were characterized by partial or complete lack of musculature, internal structures, etc, or were partially damaged due to decay (not net damage). Since Daphnia pulex appeared to suffer heavy net damage in all tows, no attempt was

made to categorize its condition.

RESULTS

Table 1 lists the particulars for all net collections made. The results for the Cladophora sampling are discussed separately from those for the crustaceans.

Cladophora drift

Table 2 presents the quantitative estimates of Cladophora drift, based on 22 collections from Mile 20 to Mile 223.

Figure 2 presents the same data graphically. The wide scatter, plus the limitations of the quantitative estimates due to flow meter problems, make any statistical evaluation of the data questionable. The trend, however, is for decreasing quantities with distance down river. The very low values at Mile 73 (22 June) are probably due to the low river flow of 21 June (Figure 1), which could have reduced the rate of detachment and permitted much of the remaining drift to settle.

Regardless of the presence or absence of quantitative changes, the numerical data do not describe the obvious qualitative changes in the Cladophora that occurred as distance down river increased. At Lee's Ferry, the Cladophora drifted down river in distinct clumps with filaments many centimeters long. By Diamond Creek, the algae had been broken down into small, short-filamented aggregates or individual strands less than 1 cm in length, all dispersed among other components of the detritus. The difficulty in separating the Cladophora from detritus in the

downstream reaches of the river makes these quantitative estimates too large, i.e., the decline in biomass (Figure 2) probably would be greater and more apparent had an efficient separation technique been available.

Crustacean plankton

Table 3 lists the crustacean species found in the net tows. Only the truly planktonic forms will be discussed. The other species are normally inhabitants of littoral vegetation and were not collected in sufficient numbers or in appropriate places to say anything about the relationship of their occurrence in the plankton to their normal ecology.

Table 4 is a compilation of all the counts of species abundance, standardized to numbers per 10 m^3 . Also included are the data for the numbers of copepods in poor physical condition and females carrying eggs. These data have also been presented graphically (Figures 3 - 5) to more clearly show the relationship of abundance of the species (Figure 3), percent carrying eggs (Figure 4), and total percent in poor condition (Figure 5), to distance down river. No obvious relationship of abundance (Figure 3) to discharge rate (Figure 1) is evident. As with the Cladophora data, no statistical tests for the significance of the relationships have been made.

Not counted, or shown here, were the considerable numbers of naupliar and copepodid stages of copepods captured by the $212\text{ }\mu\text{m}$ net in the mainstream at Miles 24, 64, and in the Kanab Creek terminal pool.

DISCUSSION

Cladophora Drift

Both the quantity and quality of the Cladophora drift changed with distance down river. The coarseness of the sampling intervals down the river, together with the inherent variability of the quantity transported, the extreme fluctuations in river flow, and the limitations of the sampling method, make it impossible to say whether or not the changes observed represent a continuous gradient. If discontinuities could be shown to occur, this would suggest the importance of looking for localized sources and sinks of the drift, some or all of which could have biological causes. Czarnecki et al (1976) list Cladophora as the dominant periphytic alga (excluding diatoms) at the confluence of 12 tributaries from the Paria River to Diamond Creek. These are certainly not the only sources. Clearly, however, the principal source region, in a general sense during this study, was the upper reaches of the river.

The pattern of both the quantity and quality of the Cladophora would be important factors in its significance as a food source for invertebrates and fishes, as well as its role in nutrient cycling through direct organic or remineralization links as a result of mechanical breakdown.

Rough calculations can be made pointing to the importance of Cladophora as a food source or nutrient sink. Assuming that the river transports a mean wet weight of Cladophora of 1.5 g/m^3 (from Table 1) and a river flow of 10,000 cfs, about 1500 kg/hr of algae are carried downstream from some undefined source regions.

For steady state conditions, this should equal the production rate at the sources. The abnormally high discharge rates which were occurring before and during the sampling period could make this an overestimate due to the possibility of excessively high rates of loss caused by the high flow.

If one assumes that a regression line can be drawn through the data of Figure 2 and that it reasonably represents the loss of Cladophora as it drifts downriver, an estimate of loss can be made. Assuming 2.0 g/m^3 at Lee's Ferry and 0.5 g/m^3 at Diamond Creek, 1.5 g/m^3 is somehow lost in transit. Coincidentally, this again amounts to 1500 kg/hr. Thus approximately 36 metric tons a day of Cladophora appear to be lost through actual (grazing, mechanical and biological degradation) and/or apparent (lack of capture by the net) causes.

Zooplankton

The only study that reports on planktonic crustaceans of the Colorado River within the Grand Canyon is that of Cole and Kubly (1976). Their Table 27 lists Daphnia sp., Bosmina longirostris, Diaptomus pallidus, Cyclops bicuspidatus thomasi, and Mesocyclops edax for the mainstream Colorado, and Acanthocyclops vernalis, found only at Elve's Chasm. Since they do not say how or when (seasonally) the samples were collected, or in what abundance, it is not possible to make any comments other than to note the two cyclopoid species caught in both studies (Table 3).

The obvious source of the planktonic crustaceans found in the river is Lake Powell. The Lake's suspected large resident populations could supply both the species and numbers of individuals observed. However, I have not seen the only study of Lake Powell zooplankton known to me (Stone and Rathbun 1968, 1969) and no comparisons can be made here.

It is possible that the Glen Canyon Dam penstock discharge contributes little or no plankton to the river, since the water came from an average depth of about _____ meters during the sampling period and the plankton would probably occur in abundance much above this depth. The spillway discharge during the period came from a surface layer an average of _____ meters deep. This flow may have contributed much or all of the plankton. Plankton would have continued to be present during the periods of no spillway discharge (Figure 1) due to losses from backeddies which had received plankton from the previous spillway releases. Since there is usually no spillway discharge, it is likely the high abundances observed in the river are exceptional.

An important question, however, is how to explain the continued presence of abundant plankton throughout the 225 miles of river to Diamond Creek. One would intuitively expect a sharp decrease with distance due to the turbidity and great turbulence. In fact, from evidence in the literature (reviewed by Hynes 1970) one might expect the populations to be reduced to negligible numbers after only a few 10's of kilometers. Perhaps the flow rate was high enough, relative to loss rates, to explain the presence. It is clear, however, that successful reproduction,

or at least hatching and growth, occurs for the length of the river sampled. This could have supplied at least some of the numbers captured. The evidence for this is the presence of egg-bearing females, of nauplii and copepodids in some of the 212 μ m net samples from the river and tributary terminal pools, and of fully developed spermatophores ready for extrusion in healthy Diaptomus males (only one female was found with spermatophore attached). No comparison can be made between the percentages of egg-carrying females in the mainstream and backeddies because sampling was not done in both environments at the same river mile. At Kanab Creek, National Beach, and Mile 220, samples were taken in both the mainstream and the tributary pools (an isolated backeddy pool at Mile 220). At these locations, the agreement between mainstream and pool percentages is striking (boxed in points in Figure 4). This agreement suggests that the exchange rate between terminal pools and the mainstream is high and the populations sampled are essentially the same. Thus these areas probably do not represent significant sources for plankton in the river, at least during the time of sampling.

Other evidence supporting Lake Powell as the only important source of river plankton during the sampling period is the condition of the organisms captured (Figure 5). The percentage in poor condition increased significantly with distance down river for mainstream, backeddy and terminal pool samples. As with egg carrying females, terminal pool percentages were about the same as in the mainstream, indicating the plankton in both places experienced the same conditions and are thus not separate populations.

The change in the condition of the plankton is probably a result of several coacting causes: mechanical damage due to extreme turbulence in passage through the dam and many subsequent rapids; lack of food (no gut content studies have been done); or simply an increase in water temperature. This latter factor would especially encourage the growth of the fungal and protist parasites. Not shown in Figure 4, or Table 4, is the fact that these parasites were not seen until Kanab Creek (Mile 144); their numbers then increased to Diamond Creek, becoming the dominant reason for considering individuals in poor condition.

If the healthy juveniles and reproductively-capable adults present at Mile 220 survive the remaining distance to Lake Mead, then the Lake Powell plankton may make a direct contribution to the composition of Lake Mead plankton..

In addition to the question of their role in contributing to the mainstream plankton, the terminal pools present several other interesting problems. The Little Colorado pool(s) appear to be a unique environment. Not only were only three individuals of one cyclopoid species (Eucyclops speratus; only one other individual was caught, in the Kanab Creek terminal pool) captured there, but also very few insect larvae were present. Two factors may account for this depauperate fauna. One, the unique chemistry of the Little Colorado water may not allow survival of most invertebrates (perhaps E. speratus is more tolerant than the other plankton). Secondly, the terminal bars, with rapid, shallow outflow, may preclude a significant introduction of plankton from the Colorado River. Cole and Kubly (1976) also noted the Little

Colorado as being impoverished in both species and numbers of invertebrates. They attributed this to periodic flooding and to the high calcium carbonate precipitation present.

The paucity of invertebrates in the Little Colorado terminal pools suggests that the humpback chub living there might have to forage at the boundary region between the Little Colorado and mainstream Colorado waters in order to find sufficient animal food.

In the National Canyon and Kanab Creek terminal pools, the Daphnia populations were much reduced (factors of 4 to 20) over those occurring in the adjacent mainstream. Those that did occur in the pools were all small individuals. A possible explanation for this observation would be predation due to fish (feeding selectively on larger individuals) and/or to other invertebrate carnivores. No crustaceans were found in the stomachs of four small speckled dace from Kanab Creek. Several cyclopoids were captured and preserved with partially consumed Daphnia in their feeding appendages (other samples had cyclopoids consuming cyclopoids).

Several other incidental observations from the samples are:

- 1) Diaptomus ashlandi individuals from Kanab Creek and below were slightly to distinctly orange, while all those from above Kanab Creek were a translucent white; 2) benthic ostracods (unidentified and uncounted) were collected in two samples; and 3) Gammarus lacustris was regularly caught in the plankton but in very low numbers.

All the above data, observations, and inferences are based

on the results of one set of samples taken during a unique flow regime of the Colorado River. They may represent an anomalous situation; only further sampling can resolve the question of the generality of the results.

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Date 1980	Approx. Time (Local)	Tow #	Net Mesh Size (mm)	Vial #	Max Tow Depth (m)	Boat (B) or Shore (S)	Location	Approx. River Miles	Est. River Flow 1000 cfs	Remarks
19	0900	243	212	12	1	S	Above North Canyon	20.2	24	In Shallow Mainstream
19	1300	3a44		11	2	B	Shinumo Wash	29.5	?	In eddy fence
20	1510	546		4	1	B	Nankoweap	53.2	30+	In broad back eddy
21	1230	7	212	3	1/2	S	In Little Colorado River	61.4	---	Repeated hand tows from edge of terminal pool
21	1300	8	212		Surf.	S	Exit channel of I.C.R. into C.R.	61.4	---	At color break rapid outflow
21	1700	9	212	10	1/2	S	1 mile below Hopi Salt Caves	64.0	?	In back eddy
22	1700	10411		5	4	B	Unkar Camp	72.5	8	In mainstream
23	1200	12	212	6	Surf.	S	In Bright Angel Creek	87.6	---	Nonquantitative
23	1500	13414		8	3	B	Granite Rapids	93.3	?	Edge of Mainstream
24	1400?	15		13	1/2	S	114 mile beach	114	30+	Nonquantitative
26	1300	17418		14	Surf.	S	Kanab Creek	143.6	30+	In mainstream bypass channel
26	1415	19420		15	Surf.	S	Kanab Creek	143.6	30+	In mainstream bypass channel
26	1500	21	212	17	1-1/2	S	Kanab Creek	---	---	In Kanab Creek terminal pool
26	1515	22	212	18	1	S	Kanab Creek	---	---	In Kanab Creek terminal pool
26	1615	23	212	19	Surf.	S	Kanab Creek	---	---	In rapid flow of Kanab Creek into terminal pool
27	1230	24425		21	2	B	Havasupai Creek	156.7	---	Vertical tows in terminal pool
28	0745	26427		22	1/2	S	Upper National Beach	166.4	30+	In edge of mainstream
28	0830	28		23	Surf.	S	Upper National Beach	166.4	---	In backwater pool at Creek mouth
29	1200	29430		24	Surf.	S	1 mile above Parashant Canyon	197	30+	In mainstream running through tamarisks
30	1500	29a		24a	Surf.	S	219 mile	219	32	Edge of mainstream running through tamarisks and over gravel
30	1600	30a		25	1	S	Upper 220 mile camp	220	32	In backwater pool
1 July	0800	31		26	Surf.	B	Mainstream	221	30+	Middle of river through eddies and rapids
1	0815	32		27	Surf.	B	Mainstream	223	30+	Middle of river through eddies and rapids
1	0915	33		28	Surf.	S	Diamond Creek	225	---	In rapid flow of creek. Nonquantitative.

Table 2
Colorado River: Lee's Ferry to Diamond Creek

Quantitative estimate of Cladophora drift

Tow #	Flow Counts*	m ³ † filtered	wet weight (g)	Weight m ³	River Mile	Remarks
2	969	1.83	5.5	3.0	20	
3	1680	3.18	3.5	1.1	20	
3a	1590	3.01	4.5	1.5	30	
4	854 (3100)	5.86	12.5	2.1	30	Flow meter jammed (est
5	2760	5.22	7.0	1.3	53	
6	1720 (3400)	6.43	5.0	0.8	53	Flow meter jammed (est
9	1560	2.95	5.5	1.9	64	212um mesh net; over- estimate, slow current
10	1940	3.67	1.0	0.3	73	Low river flow, ~8K cfs
11	1870	3.53	1.5	0.4	73	" " " "
13	1800	3.40	10.0	2.9	93	Overestimate, sticky flowmeter
14	1030	1.95	8.5	4.4	93	" " " "
17	3952	7.47	8.5	1.1	144	
18	3325	6.28	8.0	1.3	144	
19	1575	2.98	4.5	1.5	144	
20	2500	4.73	7.5	1.6	144	
26	1134	2.14	9.0	4.2	166	
27	1892	3.58	8.5	2.4	166	
29	3225	6.09	2.5	0.4	197	Much detritus
30	3275	6.19	3.5	0.6	197	" "
29a	5850	11.06	5.0	0.5	219	" "
31	1735	3.28	3.5	1.1	221	" " and sedim
32	1940	3.67	2.0	0.5	223	" " " "

* Calibration factor .00189 m³/count

† 366um mesh net

Table 3. Crustacean species collected in net tows in the Colorado River mainstream and tributary pools.

Copepoda

Calanoida

Diaptomus clavipes Schacht

Diaptomus ashlandi⁺ Marsh

Cyclopoida

Cyclops bicuspidatus thomasi^{**} Forbes

Eucyclops speratus⁺ (Lilljeborg)

Mesocyclops edax^{**} (Forbes)

Cladocera

Daphnia pulex Leydig

Leydigia quadrangularis* (Leydig)

Alona affinis* (Leydig)

Unidentified chydorid

Amphipoda

Gammarus lacustris* Sars

* Normally benthic or in littoral vegetation; not reported on here.

** Reported for Colorado River by Cole and Kubly (1976).

+ Not reported in Lake Mead by Paulson et al (1980).

TOW NO.	RIVER MILE	* LOCATION	VOLUME FILTERED M ³	Cyclops bicuspidatus Thomsen #	" " with eggs	" " poor condition	Mesocyclops edax #	Eucyclops operatus ♂+♀	Diaptomus clavipes ♂♂	" " ♀♀	" " poor condition	Diaptomus ashlandi ♂♂	" " poor condition	" " ♀♀	" " with eggs	" " poor condition	Daphnia pulex	TOTAL COPEPODS	% POOR CONDITION
2+3	20	M	5.0	4.0	-	-	-	-	-	2.0	-	-	-	6	-	-	4.0	0	
3+4	30	M	8.9	25.8	1.1	-	-	-	-	3.4	-	3.4	-	24.7	2.2	1.1	13.5	2	
5+6	53	G	11.7	21.4	-	0.9	-	-	3.4	4.3	-	5.1	-	26.5	-	-	25.6	1	
7	61	T	5.5	-	-	-	-	3.6	-	-	-	-	-	-	-	-	-	-	
9	64	B	3.0	740	140	6.7	3.3	-	6.7	6.7	-	43.3	3.3	237	23.3	30.0	56.7	4	
10+11	73	M	7.2	403	-	-	-	-	-	2.8	-	4.2	1.4	33.3	-	5.5	37.5	9	
13+14	93	M	5.4	70.4	11.1	1.9	1.9	-	1.9	3.7	-	7.4	-	38.9	-	5.6	11.1	6	
17+18	144	M	13.8	223	19.3	2.8	3.6	-	5.1	11.6	2.2	10.2	8.3	182	2.8	22.0	281	7	
19+20	144	M	7.7	274	15.2	25.3	1.3	-	5.2	23.4	1.3	11.6	-	344	-	60.8	284	11	
21	144	T	4.6	1032	63.9	9.1	-	2.2	-	4.3	-	59.3	27.4	676	18.3	36.5	13.0	3	
22	144	T	5.7	312	32.5	-	-	-	-	1.8	-	22.7	-	169	-	13.0	10.5	2	
24+25	157	T	5.7	273	11.1	7.4	-	-	-	1.8	-	7.4	3.7	129	-	3.7	21.3	3	
26+27	166	M	5.7	360	31.6	24.6	3.5	-	3.5	17.5	-	17.7	8.8	349	3.5	24.6	275	6	
28	166	T	3.2	213	18.8	12.5	3.1	-	3.1	3.1	-	16.0	18.8	297	3.1	37.6	62.6	10	
29+30	193	M	12.3	104	3.2	14.6	1.6	-	2.4	0.8	-	40.5	4.1	95.6	0.8	25.1	30.8	18	
29+30	219	M	11.1	828	12.6	5.4	1.8	-	1.8	7.2	1.8	38.7	11.7	67.5	-	17.1	46.8	12	
30+31	220	T	6.2	54.7	8.1	11.3	1.6	-	-	-	-	32.2	3.2	70.8	-	12.9	35.4	17	
31	221	M	3.3	145	21.2	27.3	-	-	-	6.1	-	78.8	15.2	191	3.0	57.6	78.8	24	
32	223	M	3.7	146	16.2	13.5	2.7	-	-	5.4	-	83.7	8.1	149	-	21.6	116	11	

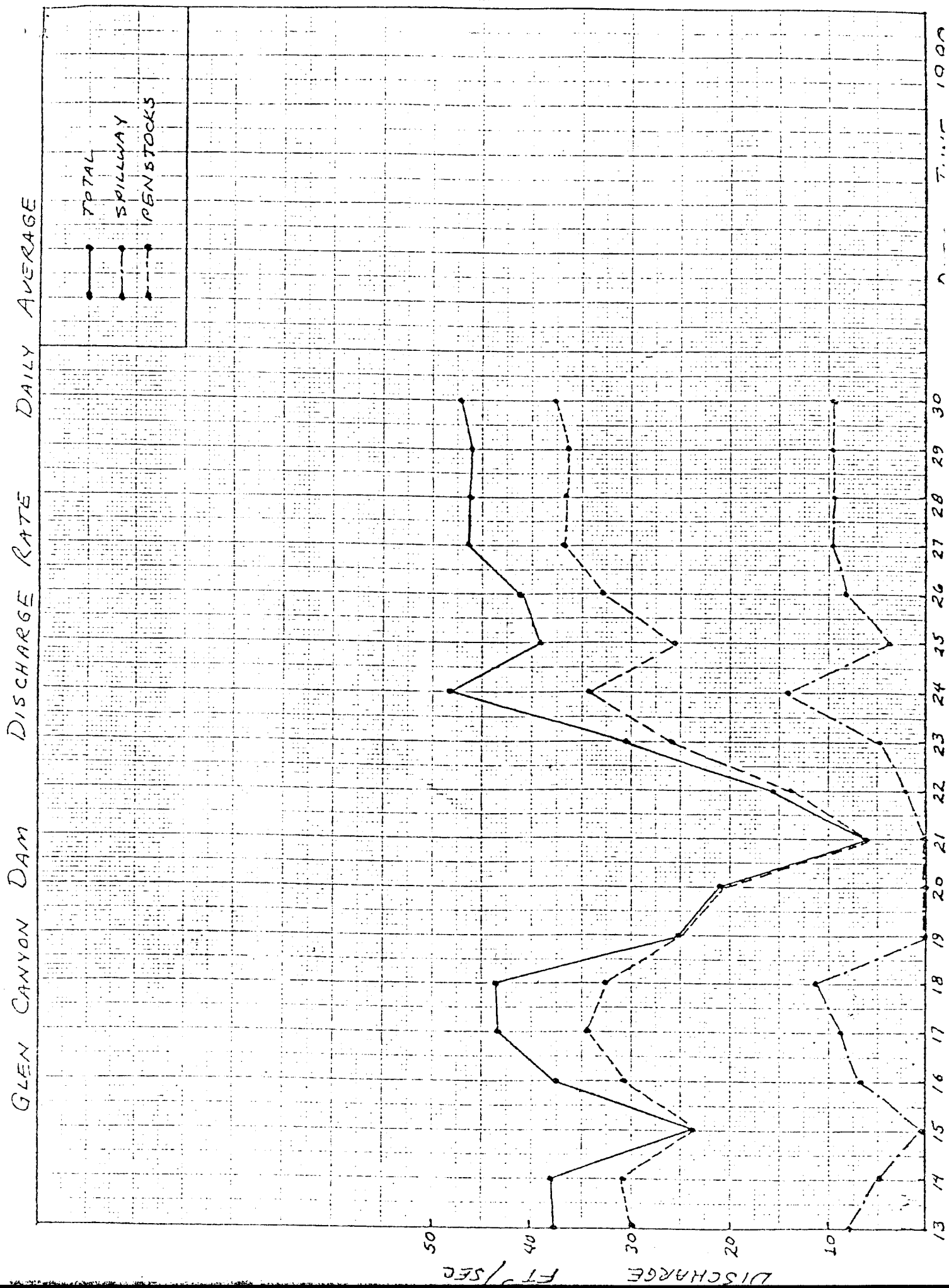
* M = MAINSTREAM

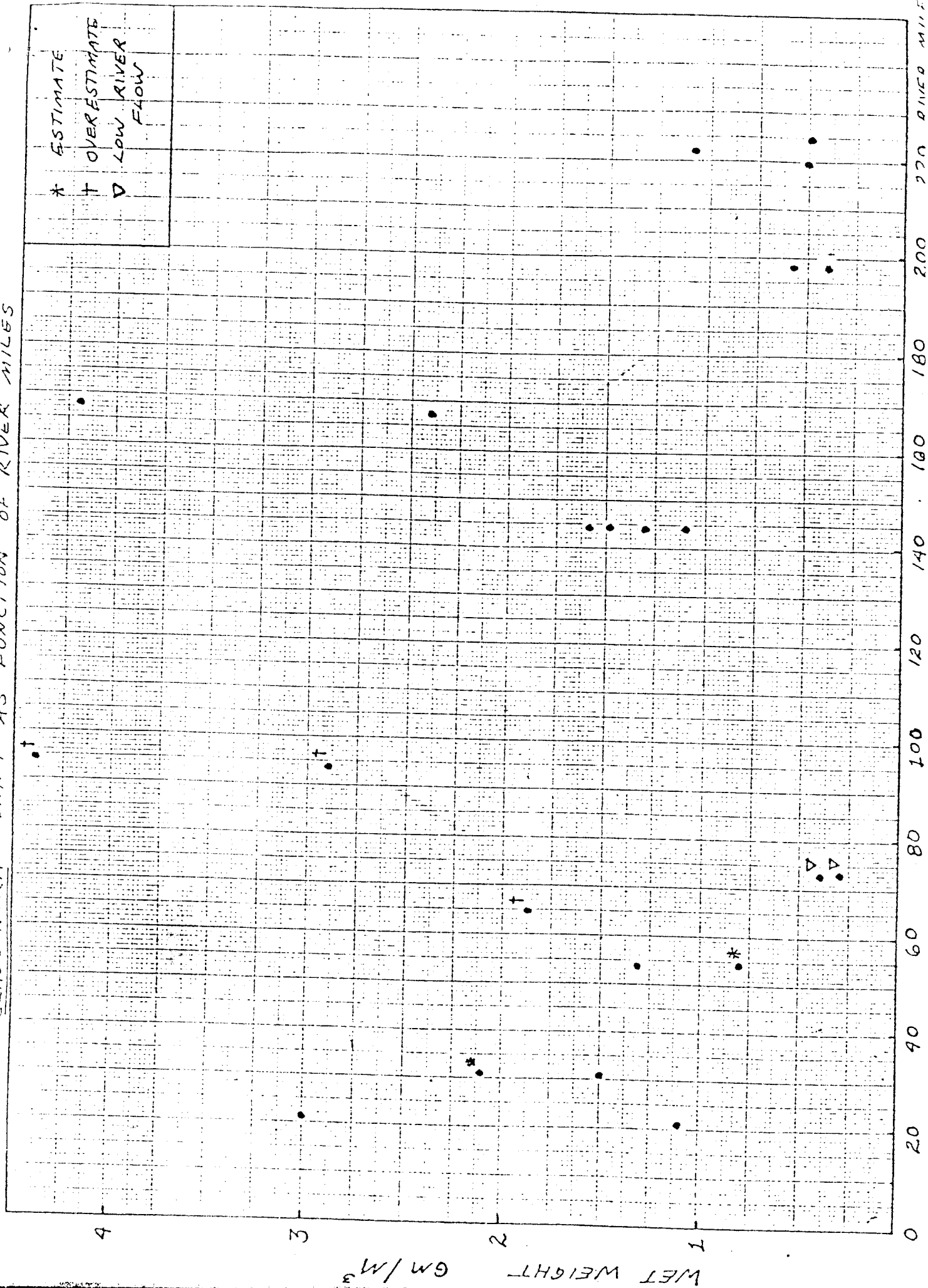
B = BACKEDDY

T = TRIBUTARY POOL

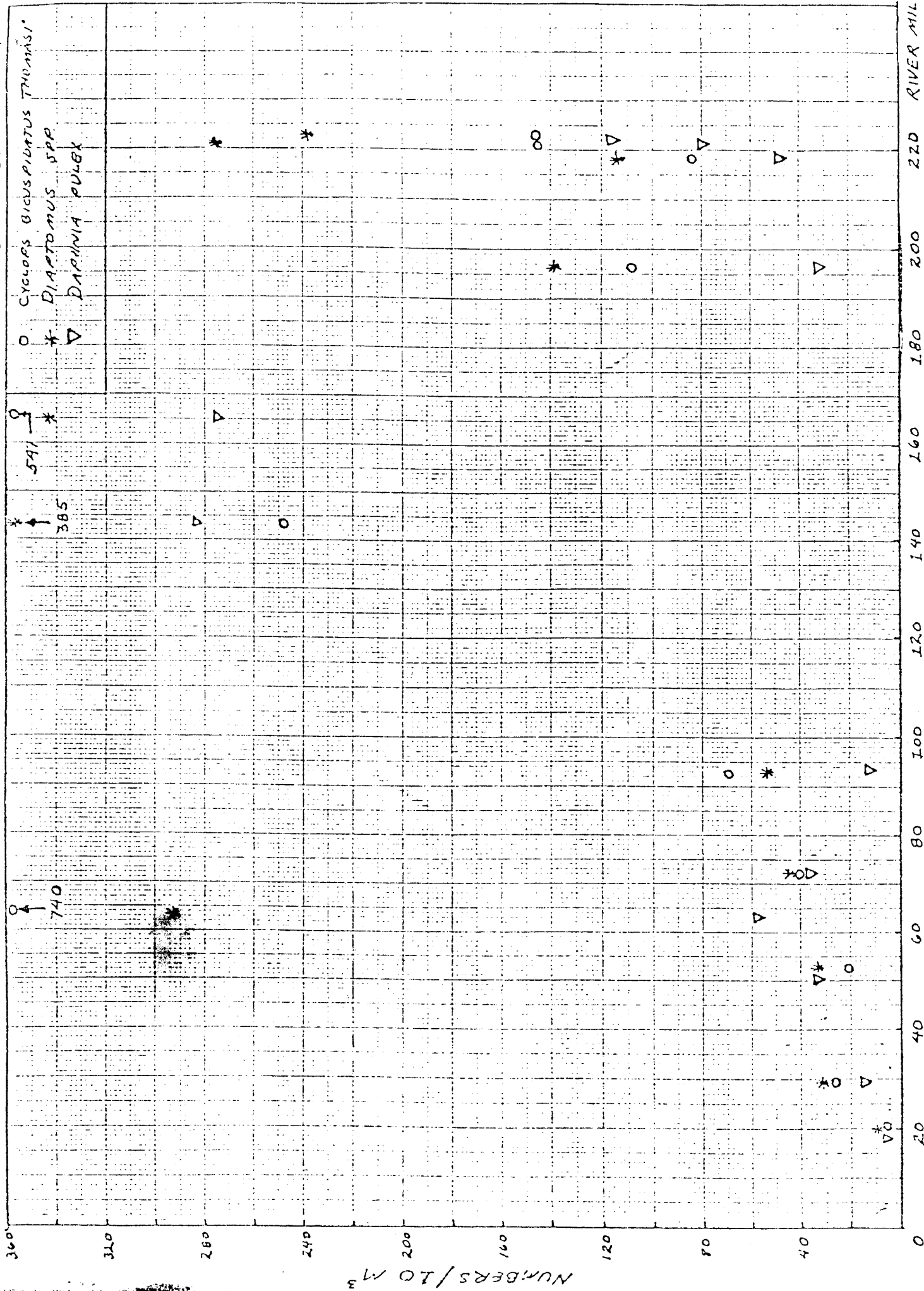
T PLUS FUNGI AND PROTISTS

FIGURE 1

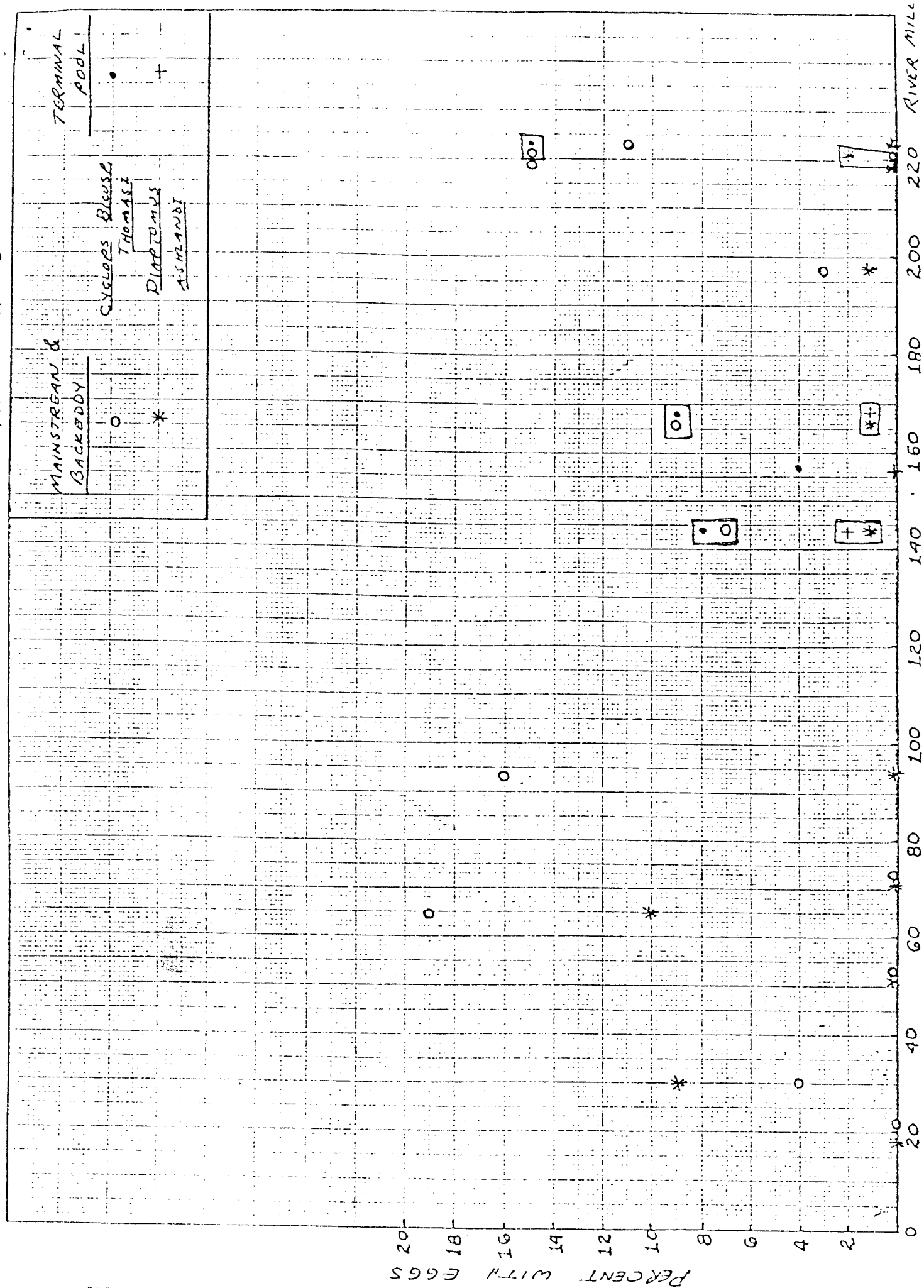


CLADOPHORA DRIET AS FUNCTION OF RIVER MILES

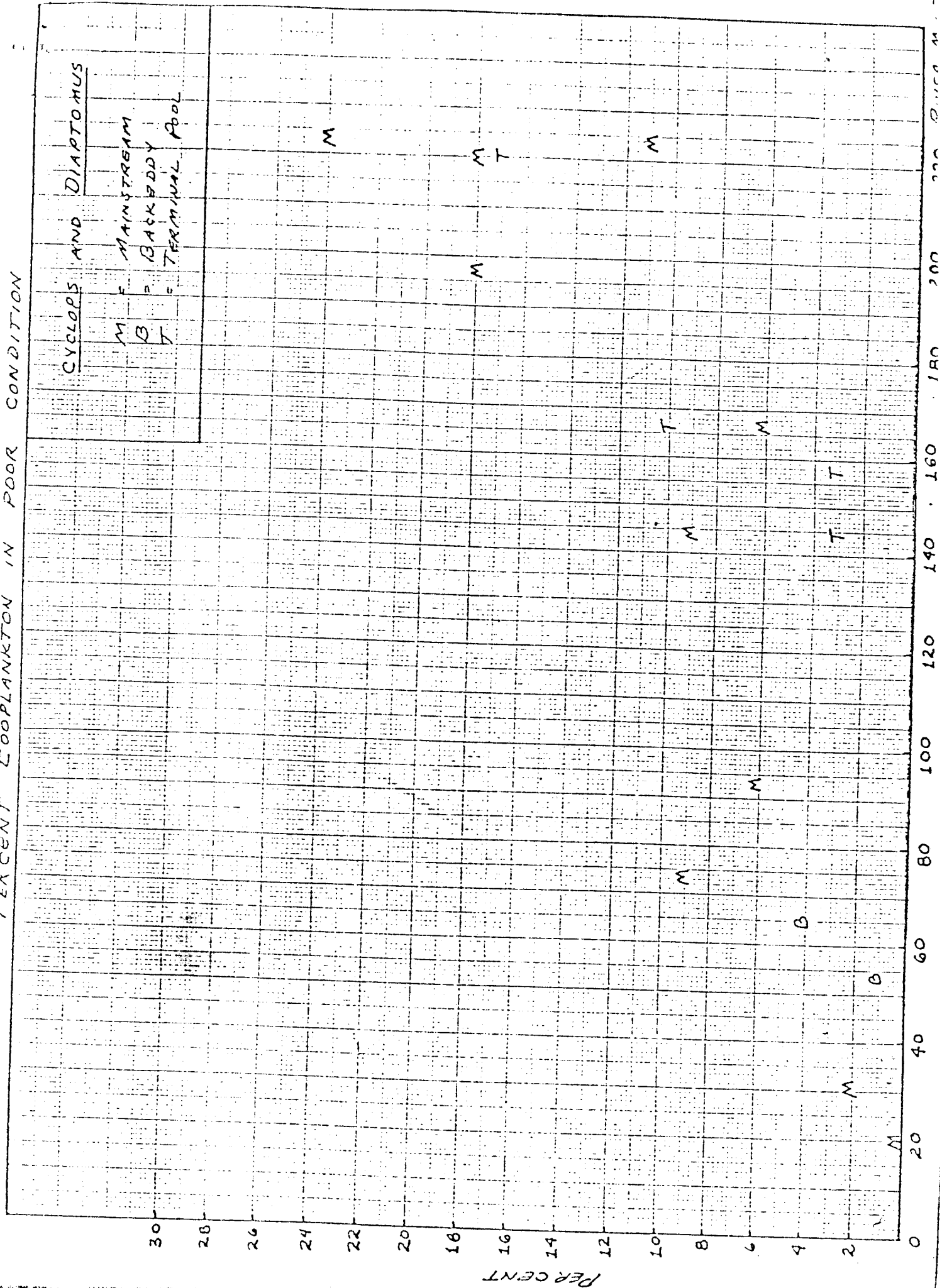
ADULT CRUSTACEAN ZOOPLANKTON AS FUNCTION OF RIVER MILES AS FUNCTION OF RIVER MILES AND MAINSTREAM AND BACKEDDIES ONLY



PERCENT ZOOPLANKTON WITH EGGS AS FUNCTION OF RIVER MILES



PERCENT ZOOPLANKTON IN POOR CONDITION



APPENDIX

SAMPLING IMPROVEMENTS NEEDED

CLADOPHORA

Equipment:

- 1) Net of about 1 to 2 mm mesh to reduce clogging problems.
- 2) Two flow meters, preferably of different types to insure volume filtered is measured.

Techniques:

- 1) Replicate samples (2-3 minimum) at each station.
- 2) A measure of quality, both physical (size?) and chemical (nutrient content, degradation products?).

PLANKTON

Equipment:

- 1) Two-flow meters, as with Cladophora.
- 2) Fine mesh net (180 μ m or less) for smallest stages (usable only in low sediment waters).

Techniques:

- 1) Replicate samples.
- 2) More midstream samples, if possible above and below rapids (deep holes).
- 3) Samples from the Glen Canyon Dam discharge.

FURTHER RESEARCH

CLADOPHORA

Attempt at a Cladophora "budget".

- 1) Measure quantity and quality of drift better.
- 2) Sources: benthic sampling, along mainstream and in confluence with tributaries; relative importance of each.
- 3) Sinks
 - a) Where does breakup occur; vegetation, rapids, etc?
 - b) What is residence time in backeddies?
 - c) Quantify loss to hangup in vegetation during high water.

- d) Animal consumption: amphipods, trout, etc.
- e) Useability as function of form.
- 4) Recycling through degradation and consumption back to nutrient pools.

ZOOPLANKTON

Study of Lake Powell plankton, both for its own interest and as source of the Colorado plankton.

- 1) Seasonality
- 2) Depth distribution

Time series over a year of mainstream and tributary plankton (quarterly or more often).

- 1) To see if the results reported here are abnormal.
- 2) Are there endemics in tributary pools--implies successful reproduction.
- 3) Quantify mortality and identify its sources down river.
- 4) Relationship of zooplankton to larval fish.

Short-term time series (several times a day for week or more).

- 1) Quantify variability in mainstream to relate to the Glen Canyon Dam discharge.
- 2) Establish exchange rates (water, sediment, plankton) between mainstream and tributary pools, backeddies and flushing rates for tributary pools.
- 3) Evidence of reproductive success in tributary pools.

"Lab" type experiments done in the field.

- 1) Survival of mainstream plankton in Little Colorado water.
- 2) Larval and juvenile fish feeding on zooplankton.